ON THE AIR-BLADDER OF FISHES.

BY CHARLES MORRIS.

The generally accepted explanation of the use of this singular organ, that it serves to enable the fish to readily rise and sink in the water, while it is in all probability true in a measure, has undoubtedly been too greatly extended. It is usually offered as applying generally to fishes with an air-bladder, with little regard to the fact that in many cases the air-bladder is too small to serve any useful purpose as a gravity organ. This being the case, some further examination into its functions and organic relations seems not amiss.

Cuvier tells us that "the most obvious use of the swim-bladder is to keep the animal in equilibrium with the water, or to increase or reduce its relative weight, and thereby cause it to ascend or sink, in proportion as that organ is dilated or compressed. For this purpose, the fish contracts the ribs or allows them to expand." This is, however, not always the case, for in many cases the bladder is provided with compressing muscles, and, as Van Der Hoeven says: "In many fishes it is difficult to show how they are in a condition to expand the bladder and to rarefy the air." Cuvier says further: "With regard to the presumed assistance which the swim-bladder affords in respiration, it is a fact that, when a fish is deprived of that organ, the product of carbonic acid by the branchiæ is very trifling; but there is no sufficient foundation for assuming that it offers any analogy to the lungs." This is no doubt true as regards the usual condition of the organ. It may perform some function in facilitating the exchange of gases in the blood, but this is not a direct respiratory function. In some cases, however, its function is directly respiratory, and in a few instances it constitutes an actual lung, closely approaching the Batrachian lung in organization.

A similar view is offered by the latest writers. Günther, in his "Study of Fishes," remarks that "this organ serves to regulate the specific gravity of the fish, to aid it in maintaining a particular level in the water, in rising or sinking, in raising the front part of its body or depressing it as occasion may require." This theory is based on hypothesis, since it would be no easy matter to prove or disprove it by experiment. As above said, however, it is in consonance with physical laws in certain cases, and in such cases it very probably gives a correct view of the function of the organ. Yet there are many cases in which the small size of the organ must render it nearly or quite useless for any such purpose, while its entire absence in very many instances of active species of fish, shows that this function is of no special value to the fish tribe as at present constituted, and suggests that the original purpose of the air-bladder must have been very different from that here surmised. A general examination of the subject may aid us in gaining some definite conception of the character of this original function.

The air-bladder of fishes is an internal sac, occupying usually the dorsal aspect of the body, and in some cases connected with the intestinal canal by a pneumatic duct, though in the great majority of cases this duct is wanting, or its cavity is closed. Thus, most generally, the bladder is a closed sac, containing gas which could only have come from the blood-vessels, with which it is abundantly provided in the form of *retia mirabilia*. This gas, in fresh-water fishes, is nearly pure nitrogen. In ocean fishes, particularly the deeper swimmers, oxygen is in excess, and has been found in some instances to constitute as much as 87 per cent. of the contents. Some naturalists advance the singular theory that the absolute weight of the fish may be increased or diminished by compression or dilation of this gas, as if the same quantity of gas could change its weight by a variation in its density. But that the relative weight of the fish, or its displacement of water, might be changed by a variation of its body-volume, through a variation in the state of compression of the air-bladder, is unquestionable, though in those numerous cases where the bladder is very small its influence must be of very little aid in the movements of the fish.

In addition to its use in aiding the fish to ascend or descend in the water, its dorsal position must also act to keep the back of the fish uppermost. In certain cases it also doubtless subserves another gravitative purpose—that of elevating or depressing the anterior region of the body, at the will of the fish. This is possible in those cases in which the bladder has a considerable longitudinal extension. In some cases, it is prolonged into the tail of the fish. In others, it sends processes into the head. And in certain instances, the ductless bladder is divided by constrictions into two or three compartments, in the longitudinal direction. In these cases, the fish may have the power to shift the gaseous contents of the bladder forward or backward at will, and thus, by a variation in the weight of the different regions of the body, to change its line of motion from a horizontal to a more or less inclined direction. Yet such a function cannot be of any absolute importance to the fish, or preparation for it would be far more general than we find it.

If we consider the conditions under which the air-bladder exists in fishes, it becomes exceedingly doubtful that it was originally evolved as a gravity-organ. In one important order of fishes, the Elasmobranchs, it does not exist. No shark or ray possesses this organ. In the main body of the fish tribe, the Teleostean, its occurrence and character are very irregular. In those which possess it, it exhibits an extraordinary variation in shape, size and relations to the body, and this sometimes between closely related genera and species. With some Teleosteans the air-bladder has an open pneumatic duct, connecting with the œsophagus, or in a few cases with the stomach. With others this duct exists, but its cavity is closed. In some cases it is reduced to a fine ligament. In many others no trace of it exists. The air-bladder itself is a hollow sac, composed usually of two tunics, and compressible, in whole or in part, by the aid of muscles on its external surface, or by other means. It is situated in the abdominal cavity, above the intestinal canal, and outside the peritoneal sac, its ventral surface being invested by a fold of the peritoneum. In some fishes it is almost loose in the abdominal cavity. In others it is intimately adherent to the vertebral column and the abdominal tissues. In many cases it is enclosed in osseous capsules formed by the vertebræ, which seem capable of exerting a pressure upon it. In addition to the cases of its longitudinal division into chambers, it is sometimes composed of two lateral divisions, and in some families there is an extraordinary development of lateral appendages.

Its occurrence is as irregular as its shape and relation to the body. In this respect, it varies remarkably in species of the same genus. Thus the mackerel has no air-bladder; yet one exists in *Scomber pneumatophorus*, a species which in every other respect very closely resembles the mackerel. So *Polynemus* *paradiseus* is without an air-bladder, while all other species of the genus have one. The same condition occurs in related genera. Thus in the species of *Sebastes* the air-bladder is very large, while in the next genus of the family it is scarcely the size of a pea.

These examples will serve to show the great diversity in the shape, size and condition of this organ. And it may be said here that these variations have no appreciable effect upon the velocity and activity of the fish. Those that have no air-bladder seem in no respect at a disadvantage, as compared with those that have one. Again, it may be said that no animal organ whose function is of known importance presents such extraordinary modifications. In the heart, lungs, brain, etc., there is one shape, position and condition of greatest efficiency, and throughout the lower forms we find a steady and undeviating advance towards this condition. There is in all these organs a persistent movement towards homogeneity; not towards heterogeneity, such as we find in the air-bladder. The natural conclusion from this would be that the air-bladder is not an organ of functional importance, while its absence from many fish, and great diversity in others, indicates that it is of minor value to the fish tribe. If it is of absolute necessity to any fish as a gravitating organ, why is it not necessary to all, and why has it not developed into some shape and condition of greatest efficiency? The existence of the air-bladder is proof that it has had, at some time, a function of considerable importance; but its many variations go to prove that it has ceased to perform any essential function, and is on the road towards extinction. On no other theory can we explain its great diversity in nearly related species.

That the air-bladder is degenerating we have evidence in cases like that above mentioned, where it is no larger than a pea. It is difficult to imagine that this minute organ is of any use to the animal. But no process of evolution can take place, except the organ is of use at every stage of its development. The natural conclusion is that the air-bladder evolved long ago, under some influence not now active, and is now on the road towards extinction, being retained only in those forms where it serves some minor purpose, but being nearly or quite obliterated in forms in which it is put to no practical use. This secondary use of degenerating organs is not uncommon. We have one instance in point in the adaptation of the embryonal gill-arches of mammals to other uses. Of these secondary employments of the air-bladder one seems to have some connection with the organ of hearing. Another seems to be to change the direction of the fish-body from the horizontal towards the vertical line. As a general rule, when present, it may fix the special buoyancy of the fish-body, and, by its situation near the back of the fish, may aid to keep the dorsal surface upward in the water. This may be the purpose of its lateral appendages, as the former is of its longitudinal extension. Yet the fishes which have no air-bladder seem none the worse off in any of these particulars. It is impossible that such an organ could have developed to perform functions which were satisfactorily performed without it, and it seems more probable that it is an organ arrested at various points in its process of degeneration, as it proved serviceable in some minor function.

If, then, we may look upon the air-bladder as an organ which has partly or wholly lost its original function, the question follows, what was that function? There are certain good reasons for believing that the breathing of air was the original purpose of this organ. In mature Teleosteans this is occasionally indicated by the existence of a pneumatic duct connecting with the œsophagus. It is true that this duct is usually of no functional use, and varies from partial to complete disappearance. But the fact is, that all fishes with an air-bladder possess a duct in the early stage of embryological development. In the mature stage it is lost by all Teleosteans except the Physostomes.

Thus embryological evidence indicates that one original function of the air-bladder was the introduction of external air into the body, a function which has now lost its importance. And the apparatus for compressing and dilating the bladder may have been originally developed as an aid in this function. Also the extraordinary development of *retia mirabilia*, in the inner tunic of many air-bladders, now used only to secrete gas into the interior, may be a survival of ancient pulmonary capillaries, which have changed their character with their function.

There are other reasons beyond those here given that the air-bladder was originally an air-breathing organ. Embryology points back to the condition of the primal fishes. But of these antique vertebrates we have existing representatives in the Ganoids and the Elasmobranchs, and it is of interest to find that in these modern survivals of the ancient fish life, the Elasmobranchs are entirely destitute of air-bladders, both in the mature and the larval stage, while all Ganoids possess an air-bladder, which retains a fully developed pneumatic duct in the mature stage. And in the suborder of Dipnoi, the air-bladder is functionally active as a lung. It is well-known that counterparts of the modern Dipnoi existed in the Devonian age, and it is highly probable that they breathed air then as they do now. In fact, we have some warrant for the belief that the antique fishes were divided into two orders, as clearly by their breathing habits as by other characteristics, the Elasmobranchs breathing by gills only, while the Ganoids had developed a supplementary organ for an occasional breathing of the air.

If we compare the air-bladder with the lungs of the higher vertebrates, we find that its general condition in the Ganoids is that of a single cavity, with an effective duct opening into the dorsal side of the œsophagus. But there is an exception to this in the Dipnoi, and in *Polypterus*. In these, the duct connects with the ventral side of the œsophagus, as in the lungs of higher animals. Wilder shows that there is a series of forms, mostly Ganoids, leading from *Amia* and *Lepidosteus*, with the pneumatic duct entering the throat on the dorsal side, to *Lepidosiren*, in which it enters on the ventral side, as in lung-breathing animals.

In all the fishes just named the air-bladder functions as a lung. In *Polyterus* it has lateral divisions, and is probably used in air breathing, while in the Dipnoi it becomes a functional lung. In *Lepidosteus*, the American Gar-Pike, the air-bladder becomes cellular and lung-like. This fish keeps near the surface, and may be seen to emit air-bubbles. It apparently takes in a fresh supply. The American Bow Fin or mud-fish (*Amia*) has a bladder of the same lung-like character, and it has been seen by Wilder to come to the surface, open its jaws widely, and apparently swallow a large quantity of air. Wilder remarks that "so far as the experiments go it seems probable that, with both *Amia* and *Lepidosteus*, there occurs an inhalation as well as exhalation of air at pretty regular intervals, the whole process resembling that of the *Menobranchus* and other salamanders, and the tadpoles, which, as the gills shrink and the lungs increase, come more frequently to the surface for air."[1]

The Dipnoi have the air-bladder developed into a true lung. Of these the Australian lung fish (*Ceratodus*), has but a single air-bladder, but this is provided with breathing pouches that possess a symmetrical lateral arrangement. It has no pulmonary artery, but receives branches from the *Arteria cœliaca*. It is supposed that this fish ordinarily breathes with the gills, but uses its lungs when the water has become thick and muddy, or is charged with gases from decomposing organic matter. Finally *Lepidosiren* and *Protopterus* have completely formed lungs, divided into two lateral chambers, and provided with a pulmonary artery. Their cellular structure nearly approaches that of the batrachian lung.

The facts here cited certainly seem to lead to the conclusion that the air-bladder was originally developed as an air-breathing organ, and only became adapted to other purposes when it had become no longer of value in this direction. We may find evidence in favor of this conclusion in the condition of the fishes which still use it as a breathing organ. With them the gill is the ordinary breathing apparatus. The lung is not called into use except when the water becomes foul or unaerated. It is a supplementary organ, which could be easily dispensed with if the fish should gain the habit of swimming in search of better aerated water. It is impossible to imagine that the air-bladder developed into a lung under the force of such a minor necessity as this. It is very much more probable that it was once an important breathing organ with these fishes, and has retained its functional value from its occasional use, but has become of minor importance, and has been largely superseded by the gill.

If now we ask, what were the conditions of life under which this organ was developed, and what were the later conditions which rendered it in great measure or entirely useless, some definite answer may be given. The question takes us back to the Devonian and Silurian geological periods, during which it is probable that its original development took place. In this era the seas were thronged with fishes of two distinct orders, the Elasmobranchs and the Ganoids, the former without, the latter with,

[1] For other instances of the same character, see Semper's "Animal Life," Note 75.

an air-bladder. This difference in organization was probably the result of some marked difference in their life habits. The Ganoids may, in their original state, have inhabited poorly aerated waters or waters otherwise ill-adapted to breathing, while the Elasmobranchs may have had their primordial habitat in clearer and purer waters.

But there were other conditions which may have been the main influencing causes in the development of an organ for air-breathing. We know that the land was habitable during long ages ere it gained any vertebrate inhabitants. The presence of insects in Devonian and Silurian strata proves this. It must have possessed much food material, both vegetable and animal, and it is hardly probable that the active fish forms of the early seas made no effort to obtain a share of this food. Long ages passed during which we have no evidence of land animals higher than insects or snails. It is highly probable that many fishes gained the habit of leaving the water temporarily for the land in search of food during this period. We know that many fishes do so now, and that some even climb trees, in spite of the many dangerous foes that now exist on land. In the era referred to there were no such dangerous foes. Such fishes as left the sea for the land would find only food to repay their enterprise. Thus there must have been a powerful inducement for fishes to assume this habit.

The indications, however, do not lead to the idea that the original development of an air-breathing organ was due to occasional visits from sea to shore. Such an organ must have slowly developed under the pressure of less extreme changes of conditions. It probably arose through the effect of such influences as still act upon fish, and force them to occasionally breathe air; such as foul or muddy water, or a lack of proper aeration arising from any cause. Another important influence is the drying-out of pools, by which fish are left in the moist mud until the recurrence of rains, or are even buried in the dried mud for the six months of the dry season. Such is the case with *Lepidosiren*, which uses its lungs during this period. In certain other fresh-water fishes, of the family Ophiocephalidæ, air is breathed while the mud continues soft enough for the fish to come to the surface, but during the remainder of the dry period it remains in a torpid state. In these fishes the air is breathed into a simple cavity in the pharynx, whose opening is partly closed by a fold of the mucous membrane. In the family Labyrinthici the accessory breathing cavity becomes an organ, with thin laminæ or plates, which undoubtedly perform an oxygenating function. This organ is greatly developed in *Anabas scandens*, the Climbing Perch. In addition to these there are cases in which fish leave drying pools, and migrate for a considerable distance overland in search of water, with no breathing organ but the gills.

If even now, when the land is everywhere occupied with active and dangerous foes, so many fish find occasion to venture on shore, it is quite probable that in the early period, when it could be visited without danger, very many fishes may have paid temporary visits to the land. And if now, under this influence, and that of drying pools and stagnant water, many fish have acquired a partial air-breathing habit, this was far more likely to take place under the more favorable conditions of ancient times. It seems quite possible that the development of the air-bladder was due to influences of this character. The occasional habit of breathing air is quite common with fish, especially of fresh-water species. Cuvier remarks that air is perhaps necessary to every kind of fish; and that, particularly when the atmosphere is warm, most of our lacustrine species sport on the surface for no other purpose.

It may be even possible to draw a hypothetical scheme of the original process of development of the air-bladder as a breathing organ. Embryology indicates that its existence began in an eversion of the intestinal canal, in its œsophageal portion, and that this gradually became an air-bladder with its pneumatic duct. It may have had its primal form in a simple pharyngeal cavity, like that of the Ophiocephalidæ, partly closed off from the food-passage by a fold of the mucous membrane. A step further would reduce this membraneous fold to a narrow opening, leading to an inner pouch. From such a condition the development of the Ganoid air-bladder, with its pneumatic duct of greater or less length, is a probable and natural one, and is sustained by embryological evidence. Though we do not possess the intermediate steps, and the breathing organ of the Labyrinthici is a specialized apparatus aside from this line of progress, yet the breathing pouch of the Ophiocephalidæ is in the direct line of development of the Ganoid air-bladder. We can scarcely look upon it as in any sense a survival of the archaic air-breathing organ. It is more probably a modern reproduction from the action of similar causes, of the first existing stage of an air-breathing apparatus. And though it is hardly probable that the reproduction is an exact one, yet it may not be very divergent from the original organ. Thus from a simple pouch in the wall of the œsophagus may have arisen, by successive steps, the air-bladder, with its pneumatic duct, its compressing muscle and its plexus of blood capillaries. And this may have unfolded, through further successive steps, several of which yet exist, into a lung like that of *Lepidosiren*. Thus we seem to possess existing representatives of every important phase in lung development, from that in which the simple wall of the intestine performed an air-breathing function, to the lung of the batrachian.

In this view of the case, the original lung was a simple, smooth-walled bladder, provided with abundant vessels to subserve blood-aeration, with muscles to aid in inhalation and exhalation, and with an air-duct opening into the œsophagus on its dorsal aspect. This dorsal connection may have arisen from the upward pressure of the air in the swimming fish, which would tend to give this position to the original intestinal pouch. But when any fish came to frequently visit the shore two new influences necessarily came into play. The effect of gravity on the growing organ would tend to drag it and its duct from the dorsal to the ventral position. And the increased use of the bladder in breathing must have required a more extended surface. It first grew cellular, then the cells became laterally-arranged pouches. Finally a constriction of the wall separated these lateral pouches, and two chambers were produced. Of every stage of this process instances still exist, and there is much reason to believe that the development of the lung followed the path here pointed out.

At the opening of the Carboniferous era there may have been many lung- and gill-breathing Dipnoi, finned Batrachians as we may call them, who spent much of their life on shore. And their habit of land-life would naturally be attended by a gradual change of the fins into better walking organs, from which by a long continued process of evolution, may have arisen the leg and foot of the primordial batrachian. For this purpose to become fully achieved, however, the development of an internal bony skeleton was necessary, and with the completion of this step of evolution the lung-breathing fish probably directly unfolded into the batrachian. But from that time forward the dominion of the fish on the land must have steadily decreased. The fin could not compete with the leg and foot as an organ of land motion, and the Dipnoid fishes were probably driven back to the water. As a result of this change of condition a retrogressive evolution took place in the air-breathing organ. Some fishes continued to use it occasionally as a lung, of which we have instances in the modern Dipnoi. Yet with the Ganoids, as a rule, it probably never attained a lung-like development, and was used only for temporary breathing purposes. This is its condition in most of the few existing Ganoids. But with their successors, the Teleosteans, it has lost all air-breathing capabilities, and has passed through every stage of degeneration, from a condition closely resembling that of the Ganoids to complete extinction. And in this process of degeneration it has been, in certain cases, adapted to minor uses, some of the most probable of which have been above enumerated, while there may be others as yet unknown to us.

A consideration of the gaseous contents of the air-bladder may lead to a conception of one such possible use. It is somewhat remarkable that it contains nearly pure nitrogen in fresh-water forms, while in the deep-swimming sea fish oxygen forms its main contents, often to a very large percentage. There must be some sufficient cause of this difference of contents. It is not due to any difference in the gases contained in water at various depths, for the percentage of nitrogen is closely the same at all depths, while oxygen diminishes in quantity from the surface downward. Thus, if its contents depended on the relative quantity of gases present, nitrogen should predominate below as well as above. It is probable, however, that the presence of oxygen in the bladder of deep-sea fishes is really due to the smaller quantity of oxygen there present in the water. The bladder may serve as a complementary aerating apparatus, as suggested by Semper, a reservoir of oxygen for the use of the fish during sleep, or when, from any cause, not actively breathing, or in poorly aerated water. Such a function would be of little or no importance to surface fish, which can readily obtain water rich in oxygen. And these fish, for this reason, may secrete only the useless nitrogen into the air-bladder. But for deep-water fishes this function may be highly necessary. When actively breathing they probably obtain little more oxygen than is required for immediate use. And the small excess gained may be secreted into the air-bladder as a reservoir, to be taken up again by the blood during inactivity of the breathing function. This seems probable from what Cuvier tells us, that when a fish is deprived of the swim-bladder, the product of carbonic acid by the branchiæ is very trifling. We cannot imagine such a result unless the bladder in some way supplies oxygen to the blood. If this be the case, the air-bladder still performs, in an indirect manner, its probable original function of a breathing organ.

If the hypothesis here offered be a well-founded one, an interesting conclusion as to the process of organic evolution involved may be taken. For we would have the air-breathing function at first performed by the unchanged walls of the œsophagus. Then this became pouched. Then the pouch became constricted off, with a duct of connection. Then the duct disappeared, as the original function vanished, and what was originally a portion of the wall of the intestinal canal, became a separate internal sac. Then this sac decreased in size, until in some instances it became a closed internal bladder, of the size of a pea, far removed from and utterly disconnected with its place of origin. Finally it completely vanished. This process, if correctly drawn, certainly forms a very remarkable organic cycle of development and degeneration, which probably has no counterpart of a similarly striking character in the whole circle of organic life.